Catastrophic Disturbances to Stream Ecosystems: Volcanism and Clear-Cut Logging

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Clear-cutting and fire are major forms of disturbance presently affecting streams in forested lands. These events have recurrence intervals on the order of decades to a few centuries. Repeated volcanic eruptions also occur in tectonically active zones such as the Pacific Northwest on time scales of centuries to millenia. Catastrophic disturbances, such as volcanism or clear-cut logging, can affect stream ecosystems in a variety of ways. Historically, research on the impacts of disturbances has been conducted on the basis of their on-site short-term impact rather than within the context of integrated, basin-level analyses. Even local impacts have not been adequately assessed from a stream ecosystem perspective. In most cases, physical and chemical attributes of water and some biotic parameters are narrowly emphasized, while other important determinants of the stream ecosystem are neglected.

Two of the most neglected components in stream ecosystem research are physical habitat and microbial processes within the sediment. In this paper, we outline the importance of physical habitat and how it is altered by catastrophic disturbance. The interaction of organic materials with physical habitat determines the kinds and rates of microbial processes in streams. We will confine our examples to the Pacific Northwest of the United States. However, these principles apply generally to forested streams everywhere. Our goal is to present a context for sampling and interpreting microbial activity in old-growth, recently clear-cut, and volcanically impacted watersheds.

CHARACTERISTICS OF UNMODIFIED FORESTED STREAMS

Unmodified streams in forests contain large quantities of large organic debris, ranging from 10 to 60 kg m$^{-2}$ (2, 6, 12, 13, 15, 20, 23, 28, 31, 32). This large organic debris shapes the stream channel by serving as dams, as temporary storage sites for sediments, organic materials, and water, and as large roughness elements causing formation of pools. Big wood in streams creates a diversity of stream habitats (Table 1). In the smallest streams in old-growth forests of the western Cascades, over 50% of the habitat is related to large wood (1, 27, 32). In larger third-order streams about 25% is created and maintained by wood. Small- to intermediate-order streams in the Panhandle National Forest of northern Idaho with gradients of 1 to 6% have 80% of the pools formed by wood (R. Rainville, personal communication).

The food base or energy supply of a stream in a forested watershed comes mainly from litter from the adjacent forest combined with algal production where high light intensity reaches the streambed. Pristine streams are also highly retentive of terrestrial organic inputs, retaining over 70% long enough for biological processing by stream organisms (19, 25, 32). The influence of the forest on energy sources and channel structure diminishes as a stream gets larger. However, the edges of a natural stream are still dominated by forest vegetation lining the banks and creating and maintaining side channels and small backwater areas, prime sites for deposition and storage of organic materials (23). Undisturbed streamside forests typically have an understory of herbaceous and shrubby plants with light gaps of various sizes. This provides the stream with a mix of coniferous and deciduous litter as well as patches of algal production. This diversity of food and habitat provides for a rich mix of species of vertebrates and invertebrates, with a full complement of age classes within species.

In addition to storing large quantities of wood, the primal stream efficiently retains smaller organic inputs and has numerous deep pools and extensive riparian vegetation. Seasonal increases in water volume result in lateral expansion rather than increases in depth because of the wood-obstructed channels. Water spreads outward and is slowed by the floodplain vegetation. This fringe floodplain in small streams helps set up many shallow littoral zones which represent a considerable proportion of the total area of the aquatic system and greatly affects productivity patterns. A motto among river biologists, "where there is no floodplain there are few fish" (38), is useful also to microbiologists because the diversity, intensity, and areal extent of aquatic microbial processes increases through floodplain interactions.
TABLE 1. Physical characteristics and disturbance impacts on small Pacific Northwest streams (1 to 3 Strahler stream orders) in old-growth forests, recent clear-cuts, and those experiencing debris torrents

<table>
<thead>
<tr>
<th>Location</th>
<th>Longitudinal profile</th>
<th>Habitat diversity</th>
<th>Organic matter storage potential</th>
<th>Quantities of downed trees</th>
<th>Shading</th>
<th>High water floodplain interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old-growth forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High gradient (&gt;4%)</td>
<td>Stepped</td>
<td>High diversity of velocities</td>
<td>High</td>
<td>High, 10–60 kg m⁻²</td>
<td>Well shaded with numerous light gaps</td>
<td>Narrow fringe but high interaction</td>
</tr>
<tr>
<td>Low gradient (&lt;4%)</td>
<td>Stepped</td>
<td>High diversity of velocities</td>
<td>High</td>
<td>High, 10–20 kg m⁻²</td>
<td>Heavily shaded</td>
<td>Very extensive</td>
</tr>
<tr>
<td>Recent clear-cut</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High gradient (&gt;4%)</td>
<td>Some steps of boulders or bedrock</td>
<td>Moderate</td>
<td>Low-moderate</td>
<td>&lt;5 kg m⁻²</td>
<td>Little shading</td>
<td>Very limited</td>
</tr>
<tr>
<td>Low gradient (&lt;4%)</td>
<td>Even grade; breaks dependent on local geology, bedrock, or ponded sand or gravels</td>
<td>Low</td>
<td>Low</td>
<td>&lt;2 kg m⁻²</td>
<td>Little shading, high light exposure</td>
<td>Low-moderate interaction</td>
</tr>
<tr>
<td>Stream experiencing debris torrent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High gradient (&gt;4%)</td>
<td>Even grade broken only by sediment deposit</td>
<td>Low</td>
<td>Low except at deposit sites</td>
<td>Very low except for deposit sites</td>
<td>Moderate; streamside vegetation scoured out</td>
<td>None</td>
</tr>
<tr>
<td>Low gradient (&lt;4%)</td>
<td>Even grade bedrock or aggraded with gravels</td>
<td>Low</td>
<td>Organic storage on the floodplain; low in channel storage</td>
<td>Moderate amounts on floodplains 2–10 kg m⁻²</td>
<td>Moderate; streamside vegetation drowned</td>
<td>Low; can be extensive on highly aggraded streams</td>
</tr>
</tbody>
</table>
The degree of floodplain influence is complex and largely determined by the extent, timing, frequency, and duration of water exchange between the stream and adjacent riparian floodplains (16, 38). Overbank flow is a natural process which builds floodplain features such as natural levees and supplies water to adjacent lowlands that serve as storage sites for excess runoff (21). Water velocities are greatly reduced during flood events in the floodplain relative to the main stream channel, because of shallower flow and greater streambed roughness. As a result, considerable deposition of sediment, organic material, and nutrients occurs in these areas. Alluvial floodplains are a sink for nitrogen, carbon, and phosphorus and are processing areas for organic matter. In addition, partially processed fragmented detritus and dissolved organic material are washed back into the main channels so that streams with complex adjacent wetlands tend to carry more organic matter than those without such features (7, 17).

CATASTROPHIC DISTURBANCES

Human manipulation. Streams throughout North America have been systematically cleaned of snags and organic debris for more than 150 years (23, 24). For example, from the middle 1800s to about 1920 large- and intermediate-sized rivers in the Pacific Northwest were cleared of drift jams and snags so steamboats and rafts could navigate the rivers, transporting supplies and agricultural products. From the 1880s to 1915 small rivers and streams were used to transport logs out of the woods to the mills. The streams had to be cleaned of debris before the logs could be driven. Many streams had several expansive splash dams on them to augment the flow enough to drive logs (24). In the 1940s and 1950s, organic debris was a big problem in Oregon and Washington streams, as streambeds were used as logging roads and harvested trees were pulled into them. These management activities have resulted in a long-term loss of habitat diversity and carbon storage, and a reduction in floodplain interaction.

Clear-cutting and timber management activities are relatively recent factors altering the structure and organic matter in streams. Clear-cut logging normally results in an increase in stream runoff, water temperature, sediment inputs, and light, and in decreases in litterfall, carbon storage, and habitat-forming large wood (Table 1). Clear-cutting is often followed by overzealous cleanup of organic debris from the stream, undertaken to "protect the fisheries" by removal of potential migration barriers. In addition, as road building associated with logging operations extends ever further into steep coun-

try, the probability of channel-scouring debris torrents increases. Debris torrents, initiated by small landslides, move catastrophically down stream channels, severely eroding the streambed. These torrents routinely cause an abrupt release of stored sediment and organic debris which eventually clumps into one spot, often scouring the upstream channel down to bedrock (Fig. 1). In one Coast Range watershed in Oregon, 30% of the first-order streams are scoured to bedrock, and 60% of the second-order streams and 40% of the third-order streams have experienced debris torrents (27). These torrents have scoured the channels and left large deposits of organic material and inorganic sediment where the gradient flattened to about 4% (27) or the tributary entered a larger stream at an angle greater than 40° (L. Benda, personal communication). In excess of 80% of these debris torrents were caused by logging activity or road failures (27). Although we tend to talk of localized impacts of clear-cutting, debris torrents can travel 1 km or more and affect several stream orders, severely reducing the capability of the stream for dispersed retention of organic material. The most active zones of microbial and biological processing then become clumped throughout the river basin instead of being more uniformly distributed throughout the drainage network (Fig. 1).

Longitudinal profiles of disturbed and undisturbed streams are illustrated in Fig. 1. Streams in old-growth forests without recent torrents maintain a stairstepped profile throughout the length of the stream. Streams experiencing debris torrents either have clumped depositional areas and a few large steps or have been altogether sluiced out and have only steps that are topographically provided by bedrock outcrops. When the depositional areas are examined in cross section or in planar view, a clearer picture emerges of the capacity for the channels to store carbon (Fig. 1). In the streams of old-growth forest, the extent of deep pools, pools at the stream margin, and side channels at low flow are commonly controlled by large wood. Where deposition and storage of organic material are concentrated, a complex mixture of aerobic and anaerobic processes degrades the organic matter. Diverse microbial processes occur throughout the stream. In streams which have been recipients of debris torrents within the past 20 years, large, widely scattered deposits of organic and sediments provide centers for microbial processing and remineralization. These environments are fewer but have larger concentrations of organic material. The small, scoured streams have microbial processes restricted mainly to algal development and decomposition. Organic material is not retained long enough nor in
adequate quantity for anaerobic processes to occur at the rates found in old-growth forested streams or within debris concentrations.

Other common forestry practices also reduce debris loading and storage relative to the undisturbed stream ecosystem. Thinning and harvest rotations of 60 to 100 years remove the future source of large debris, cutting off resupply. Management of streamsides for timber production alone totally eliminates the source of large debris. Growing demand for wood fiber also encourages the leaving of less forest residue and the exploitation of additional tree species (31).

The culmination of almost two centuries of human management and exploitation has shaped streams into ecosystems often distantly removed from primeval conditions. Erosion has increased, and debris torrents are more common. Many sections of stream have reduced storage capacity for organic material, and other sections have been inundated with inorganic sediments, lowering the overall carbon available per length of stream. Floodplains and the volume of surface water within basins grow smaller and organic-rich deposits of sediment diminish.

Volcanism. On 18 May 1980, Mt. St. Helens in southwestern Washington erupted violently. Four major zones of impact were associated with the eruption (Table 2). First, a massive debris avalanche filled the upper 26 km of the North Toutle River to depths between 10 and 195 m. This event dammed numerous streams and eliminated the drainage network in the valley. Second, mudflows associated with snow and glacial ice melt moved down four of the major drainages of the mountain. These mudflows scoured the valley bottom, and mud deposits killed many trees along the outer edges of the floodplain. The mudflows backed into and dammed most of the tributaries of the main channels. Mudflow levees also trapped ash and pumice, which were being exported down adjacent tributaries. By summer of 1981, many tributaries had ash deposits filling their valleys for 3 to 6 km above the confluence with the mudflow. This resulted in wide, shallow, very exposed channels of sand-sized sediments. Third, in the blast zone, which includes 480 km² of devastat-
TABLE 2. Extent and characteristics of volcanic events and effects on channel geometry, shading, organic matter storage, and habitat in streams affected by the 1980 eruptions of Mt. St. Helens (18; F. Swanson, personal communication)

<table>
<thead>
<tr>
<th>Volcanic event</th>
<th>Affected area (km²)</th>
<th>Deposit thickness (m)</th>
<th>Deposit emplacement temp (°C)</th>
<th>Channel geometry</th>
<th>Channel shading</th>
<th>Organic matter storage potential</th>
<th>Habitat diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Debris avalanche</td>
<td>60</td>
<td>10-195</td>
<td>70-100</td>
<td>Total destruction</td>
<td>None</td>
<td>Low; dependent on boulders or rock outcrops</td>
<td>Low</td>
</tr>
<tr>
<td>Blast</td>
<td>370</td>
<td>0.08-1</td>
<td>100-300</td>
<td>Low-moderate changes</td>
<td>Low</td>
<td>Very high as a result of down trees in channel</td>
<td>High</td>
</tr>
<tr>
<td>Seared vegetation</td>
<td>110</td>
<td>0.02-0.08</td>
<td>50-250</td>
<td>Slight local changes</td>
<td>Low-moderate changes</td>
<td>Low-moderate</td>
<td>Moderate</td>
</tr>
<tr>
<td>Mudflows</td>
<td>50</td>
<td>Mainly 2, up to 30</td>
<td>32</td>
<td>Moderately to highly altered</td>
<td>None</td>
<td>Low</td>
<td>Low</td>
</tr>
<tr>
<td>Ashfall</td>
<td>950</td>
<td>0.03</td>
<td>30 (?)</td>
<td>No major changes</td>
<td>Heavy shading</td>
<td>Moderate-high</td>
<td>Moderate-high</td>
</tr>
</tbody>
</table>

ed forest and seared vegetation, the streams were not only choked with ash and pumice, but also inundated with trees blown down by the blast. The downed and shattered trees and foliage exerted a major influence on the routing and storage of ash eroding from hillsides. In the seared vegetation zone much of the foliage dropped within a few months of the major eruption. Leachate from the organic debris and the litterfall provided large quantities of organic energy to the streams. Fourth, the greatest areal impact of the eruption was the ash or tephra-fall zone. In these streams the pristine channels in the old-growth forests were inundated with ashfalls of 5 to 20 cm. However, nearly all of the riparian vegetation survived, and channel structural features such as boulders and large downed trees were unaffected. The streams today look very much like they looked before the eruption. Dense stands of herbaceous and shrubby plants and vigorous conifers line the edges of the streams, and after the first winter the riffles had been swept clean of most of the ash. After the second winter the pools had been completely flushed and most of the ash had been deposited on the floodplain.

The streams in the blast zone experienced large inputs of both fine sediments and organic carbon. Streams with downed trees experienced no significant widening of the channel, and the channels have started to grow deeper. In reaches with heavy tree loading, much of the ash has been deposited on the floodplain or transported downstream. Over 90% of the pools are created or significantly enhanced by the large wood. Streamflow around the downed trees scours the ash, and the pre-blast cobble-gravel substrates are reappearing. Streamside shrubs and herbaceous plants are coming back quickly, but still provide just 5% of the pre-blast cover and even less carbon input after 3 years. Many of the blast-zone streams which were not salvage logged will have excellent habitat for storing and processing organic materials. In the areas without downed trees, the riffle sections have become longer, the frequency of pools has decreased, and side channels and backwaters have become filled with sediments.

In the long term (50 to 100 years), streams which had their dead riparian forests salvage logged will show little increase in carbon storage capacity. Those streams in which the dead streamside forest is left will have large areas where terrestrial carbon will be stored and be processed. Our ideas result from examining streams on nearby Mt. Rainier and Mt. Hood that had mudflows fill their valleys 150 to 250 years ago, killing the riparian forest. Because of the uniformly flat valley floor and fallen trees from the pre-mudflow forest, these streams contain large quantities of stored carbon associated with downed wood both on the floodplain and in stream channels. Downed trees from the pre-blast forest will play a major role in the restoration and maintenance of retention sites for organic matter. The channels in the valleys that received the impact of the debris avalanche and mudflow remain highly unstable and migrate through the valley annually. Little vegetation has reappeared, and sediment loads are extremely high. Sites of long-term storage of carbon and sediment are presently confined to the floodplain, and new sources of terrestrial organic matter will require decades to gain a foothold.
MICROBIAL PROCESSES

The microbial response to major disturbance within streams must be considered together with the changes in the physical structure and also the chemical composition of stream water and sediment. Important physical changes we have discussed are (i) the quantity of carbon and nitrogen stored within the channel, (ii) the amount of light reaching the stream, (iii) the retentive capacity of the channel, and (iv) the quantity of inorganic sediment eroded into the stream network. Major chemical shifts include (i) increased concentration of dissolved nitrogen and phosphorus compounds in the stream water following clear-cutting (3, 14; C. N. Dahm, Ph.D. thesis, Oregon State University, Corvallis, 1980) and (ii) the amount of allochthonous particulate carbon and nitrogen entering the stream. An understanding of the physical and chemical consequences of catastrophic disturbance provides the basis for evaluating the response of the microflora. We will limit our discussion to microbial rates within major components of the nitrogen and carbon cycle in Pacific Northwest forested streams following clear-cutting and cataclysmic volcanic eruptions. However, the rates of all microbial processes in stream ecosystems are closely intertwined with the dynamic physical and chemical changes brought about by a major disturbance, and this interplay should be considered in all studies of stream microbiology.

Measurements of algal primary production, respiration, nitrogen fixation, nitrification, and denitrification have been made in streams from an old-growth (350 to 550 year old) Douglas fir, western hemlock forest, a recent clear-cut, a stream on the main debris flow from Mt. St. Helens, and from the tree blowdown zone within the blast zone of Mt. St. Helens (Table 3).

Nitrogen cycle processes were emphasized as a result of the generally low concentrations of inorganic nitrogen in streams in the Pacific Northwest (S. V. Gregory, Ph.D. thesis, Oregon State University, Corvallis, 1980) and the apparent initial nitrogen limitation in streams and lakes throughout the blast zone of Mt. St. Helens (4, 11).

Algal primary production is often increased in smaller streams following a disturbance which opens the canopy and allows additional light to reach the streams (Gregory, Ph.D. thesis, Oregon State University, 1980). Streams in recent clear-cuts and many of the higher gradient streams near Mt. St. Helens now produce algal biomass during low flow conditions that is much larger than that in streams in old-growth forests. A comparison of net algal primary production in a third-order stream within an old-growth forest and a third-order stream within a recent clear-cut showed an eightfold higher rate in the clear-cut (37). This trend also holds for many streams affected by the eruption of Mt. St. Helens, except where highly unstable streambeds scour substrates and high turbidity limits light penetration, eliminating photosynthetic activity. In general, except in highly unstable geomorphic situations, disturbance of streamside vegetation increases microbial photosynthetic production, particularly during summer base flow.

The overall effect of disturbance on heterotrophic activity in streams is more difficult to assess. Respiratory activity in streams within the blast zone of Mt. St. Helens was exceptionally high in the first year after the eruption. Dissolved organic carbon extracted from the devastated forest by the hot blast deposits fueled heterotrophic bacteria (4). This activity has diminished markedly since 1980, and the extremely erosive channels now store carbon mainly in the lower gradient depositional areas and where

<table>
<thead>
<tr>
<th>Stream description</th>
<th>Algal primary production</th>
<th>Respiration</th>
<th>N₂ fixation</th>
<th>Nitrification</th>
<th>Denitrification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old-growth watershed, Oregon Cascades</td>
<td>Low</td>
<td>Moderate-high</td>
<td>Low</td>
<td>Low</td>
<td>Moderate-high</td>
</tr>
<tr>
<td>Recent clear-cut, Oregon Cascades</td>
<td>High</td>
<td>Low-moderate</td>
<td>Moderate</td>
<td>Low</td>
<td>Moderate</td>
</tr>
<tr>
<td>Debris avalanche, Mt. St. Helens</td>
<td>Low</td>
<td>Initially high, now low</td>
<td>Initially high, now low</td>
<td>Initially high, now low</td>
<td>Initially high, now low</td>
</tr>
<tr>
<td>Blast zone, downed vegetation, Mt. St. Helens</td>
<td>Moderate</td>
<td>Initially high, now low</td>
<td>Initially moderate, now low</td>
<td>Initially high, now low</td>
<td>Initially high, now moderate</td>
</tr>
<tr>
<td>Ashfall, Mt. St. Helens</td>
<td>Low-moderate</td>
<td>Low-moderate</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
</tr>
</tbody>
</table>
stable accumulations of large woody debris occur. Respiratory activity in the sediment is now minimal in many streams near the volcano. This is probably a result of inorganic sediment inundation and flushing of fine organic material downstream or onto the floodplain. Over 90% of the erosion of ash from hillslopes occurred during the first winter (F. J. Swanson, B. Collins, T. Dunne, and B. P. Wichterski, Erosion Control in Volcanic Areas, in press). A similar but less extreme pattern is repeated in clear-cut watersheds where an initial stimulative response is followed by decreased overall input and storage of carbon to the small streams and a new decrease in stream respiration.

Rates of nitrogen (N$_2$) fixation in small streams flowing from old-growth forests are generally quite low (8). N$_2$ fixation is an expensive process energetically, requiring either sunlight or a source of chemical energy such as organic compounds or chemically reduced inorganic material. In old-growth forests, autotrophic N$_2$ fixation occurs mainly in the forest canopy through N$_2$-fixing lichens (9, 10). N$_2$ fixation in the stream is from bacterial heterotrophs, often on wood, and rates are low (0 to 1.3 μmol of N$_2$ g$^{-1}$ of wood day$^{-1}$). After clear-cutting, N$_2$-fixing algal forms often become established. N$_2$-fixing forms of Nostoc sp. are especially prominent in clear-cuts of the Pacific Northwest. N$_2$-fixing algal species also appeared in thermal seeps throughout the blast zone of Mt. St. Helens within months of the main eruption (36). However, the unstable substrate has not favored widespread colonization of N$_2$-fixing algal forms in most streams in the blast zone of Mt. St. Helens. Levels of heterotrophic N$_2$ fixation in stream water have also been below detection (<0.1 nmol of N$_2$ liter$^{-1}$ day$^{-1}$) except for the extremely high rates (to 4.1 μmol of N$_2$ liter$^{-1}$ day$^{-1}$) the first few months after the eruption.

Numerous publications have addressed the losses of nitrate in drainage water from disturbed forest ecosystems (summarized in 34, 35). The numbers of nitrifying bacteria within the forest soil have been shown to increase after disturbances (26, 30), and rates of potential soil nitrification were strongly correlated with rates of nitrogen mineralization (22). Nitrification rates are regulated by the availability of ammonia and the concentration of dissolved oxygen (5). However, with the exception of highly polluted rivers and estuaries, few data have been published on potential or actual rates of nitrification in streams within forested watersheds.

Potential rates of nitrification within streams in the blast zone of Mt. St. Helens during 1980 and 1981 were high (up to 3.0 μg of NO$_3$-N liter$^{-1}$ day$^{-1}$). A dramatic increase in microbial numbers and activity was common to all aquatic environments in the devastated zone (4, 11). Stream waters, which remained aerobic from atmospheric resupply of oxygen, were primary sites for nitrification. Streams on the debris flows, where hot volcanic deposits were intermixed with forest soil and debris, were most active. This, however, was a transient phenomenon, and the rates of nitrification decreased to low levels as the deposits cooled and as the leaching of ammonia diminished.

The effect of clear-cutting on nitrification rates in streams has not been as well documented as in the soils. Preliminary measurements in streams in a clear-cut, alder-dominated second growth and in an old-growth watershed of Oregon found low, relatively constant rates (0.015 to 0.072 μg of NO$_3$-N g$^{-1}$ of sediment day$^{-1}$). Although greater rates of nitrification might be predicted in the clear-cut, an efficient nitrifying population within the soil could utilize the available ammonia and suppress activity within the stream. A 3-month average of twice-weekly ammonia measurements was less than 5 μg of NH$_4$-N liter$^{-1}$ for all three streams, but nitrate concentrations were highest in the clearcut. Increased concentrations of nitrate within a stream do not require a direct link to an available nitrifying population. More in situ measurements of nitrification potential associated with the sediments of forested streams are needed, in addition to the data on inorganic nitrogen concentrations after disturbance.

Denitrification can occur within stream sediments where accumulations of organic material and physical factors produce oxygen-deficient waters. Rates of denitrification are regulated by the nitrate and oxygen concentration, with less control exerted by temperature and the supply of dissolved carbohydrates (29, 33). Debris dams, side channels, beaver impoundments, pools, and periphyton communities provide habitats where this process may occur.

Potential denitrification rates in streams in the blowdown and debris-flow zones ranged from 36 to 290 μmol of N$_2$O liter$^{-1}$ day$^{-1}$ during the first year after the eruption of Mt. St. Helens. A large, active denitrifying bacterial population was established. However, stream concentrations of nitrate were near the detection limit of 3 μg of NO$_3$-N liter$^{-1}$, and these potential rates may overestimate actual rates, although a large population capable of denitrifying was present. Streams in heavy ashfall areas had increased loads of inorganic sediment, but denitrification was not detected. Measurements of denitrification rates without nitrate amendment in sediments from an old-growth forested stream were three times those in a clear-cut forest stream (0.12 versus 0.34 μmol of N$_2$O g$^{-1}$ of sediment day$^{-1}$). This was in spite of a higher concentra-
tion of nitrate in the clear-cut forest stream (135 versus 87 μg of NO₃⁻N liter⁻¹). However, the organic content of the old-growth sediment averaged 35% while the average was 5% in the clearcut. Although the majority of discussions concerning nitrate increases in disturbed forest ecosystems after clear-cutting have dealt with increases in nitrification, greater rates of denitrification in old-growth forest streams may also contribute to a decreased loss of nitrate in mature forests. Physical stability, greater retention of organic inputs, and more stored organics favor denitrification within undisturbed high-gradient forest streams.

How do these overall changes in carbon and nitrogen cycle processes affect the small high-gradient streams of the Pacific Northwest after major disturbances such as clear-cutting and volcanic eruption? First, microbial response cannot be separated from the physical processes within the watershed that affect the stream. When inorganic sediment inundates the stream channel and both short- and long-term storage of carbon are impeded, the types, intensity, and location of microbial activity also change. Second, algal production, stimulated by increased light and nitrate input, becomes more important as a food resource for the stream community if stable substrate is available and scour from sediment movement is low. Third, nitrogen loss from the watershed, mainly as nitrate, can be reduced within old-growth forested watersheds both by decreased nitrification within the soil and by higher potential denitrification in the stream sediments.

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LITERATURE CITED


